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Tedersoo, Leho

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High-level classification of the Fungi and a tool for evolutionary ecological analyses

Leho Tedersoo^{1,2,3} · Santiago Sánchez-Ramírez⁴ · Urmas Köljal^{1,2} · Mohammad Bahram^{3,5} · Markus Döring⁶ · Dmitry Schigel^{6,7} · Tom May⁸ · Martin Ryberg⁵ · Kessy Abarenkov¹

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Abstract

High-throughput sequencing studies generate vast amounts of taxonomic data. Evolutionary ecological hypotheses of the recovered taxa and Species Hypotheses are difficult to test due to problems with alignments and the lack of a phylogenetic backbone. We propose an updated phylum- and class-level fungal classification accounting for monophyly and divergence time so that the main taxonomic ranks are more informative. Based on phylogenies and divergence time estimates, we adopt phylum rank to Aphelidiomycota, Basidiobolomycota, Calcarisporiellomycota, Glomeromycota, Entomophthoromycota, Entorrhizomycota, Kickxellomycota, Monoblepharomycota, Mortierellomycota and Olpidiomycota. We accept nine subkingdoms to accommodate these 18 phyla. We consider the kingdom Nucleariæ (phyla Nucleariida and Fonticulida) as a sister group to the Fungi. We also introduce a perl script and a newick-formatted classification backbone for assigning Species Hypotheses into a hierarchical taxonomic framework, using this or any other classification system. We provide an example of testing evolutionary ecological hypotheses based on a global soil fungal data set.

Keywords 51 new taxa · Species Hypothesis · Taxonomy of fungi · Phylogenetic classification · Subkingdom · Phylum · Nucleariæ · Ascomycota · Aphelidiomycota · Basidiobolomycota · Basidiomycota · Blastocladiomycota · Calcarisporiellomycota · Chytridiomycota · Entomophthoromycota · Entorrhizomycota · Glomeromycota · Kickxellomycota · Monoblepharomycota · Mortierellomycota · Mucoromycota · Neocallimastigomycota · Olpidiomycota · Rozellomycota · Zoopagomycota

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✉ Leho Tedersoo
leho.tedersoo@ut.ee

¹ Natural History Museum, University of Tartu, 14a Ravila, 50411 Tartu, Estonia

² Institute of Ecology and Earth Sciences, University of Tartu, 14a Ravila, 50411 Tartu, Estonia

³ Estonian Young Academy of Sciences, 6 Kohtu, Tallinn, Estonia

⁴ Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St., Toronto, ON M5S 3B2, Canada

⁵ Systematic Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden

⁶ Global Biodiversity Information Facility, Copenhagen, Denmark

⁷ Department of Biosciences, University of Helsinki, Helsinki, Finland

⁸ Royal Botanic Gardens Victoria, Birdwood Ave, Melbourne, VIC 3004, Australia

Introduction

Fungi are one of the largest groups of eukaryotes that play key roles in nutrient and carbon cycling in terrestrial ecosystems as mutualists, pathogens and free-living saprotrophs (McLaughlin and Spatafora 2014). Because many fungi are unculturable and seldom produce visible sexual structures, molecular techniques have become widely used for taxonomic detection of species to understand shifts in their richness and composition along environmental gradients (Peršoh 2015; Balint et al. 2016; Tedersoo and Nilsson 2016). Accurate taxonomic identification to species, genera and higher taxonomic levels is a key for reliable assignment of ecological and functional traits to taxa for further ecophysiological and biodiversity analyses (Kõljalg et al. 2013; Jeewon and Hyde 2016; Nguyen et al. 2016; Edgar 2017; Tedersoo and Smith 2017). Furthermore, molecular methods have revolutionized our understanding concerning phylogenetic relationships among the Fungi and have substantially altered the morphology-based classification system (Hibbett et al. 2007; Wijayawardene et al. 2018). Availability of full-length rRNA gene and protein-encoding marker gene sequences (James et al. 2006a) and evolution of high-resolution genomics tools (Spatafora et al. 2016, 2017) has further refined the order of divergence and classification of the major fungal groups (e.g. Zhao et al. 2017).

Species-level molecular identification of fungi takes advantage of the Internal Transcribed Spacer (ITS) region of ribosomal RNA (rRNA) gene (Gardes and Bruns 1996; Kõljalg et al. 2005; Schoch et al. 2012; Nilsson et al. 2014). The ITS region is not, however, reliably alignable across families and higher taxa, which renders large-scale phylogenetic approaches and testing evolutionary ecological hypotheses (cf. Cavender-Bares et al. 2009) impossible. Information concerning phylogenetic distance among fungal taxa in communities enables to detect relatively subtle shifts in diversity and better understand community assembly processes (Fouquier et al. 2016). Using rRNA 18S gene sequences, Maherali and Klironomos (2007) demonstrated that phylogenetically overdispersed communities promote biomass strongest, but growth benefits of arbuscular mycorrhizal fungi are phylogenetically conserved. Rousk et al. (2010) showed that soil pH has a strong effect on fungal and bacterial phylogenetic composition on a local scale.

Depending on the target group of organisms and taxonomic resolution, plant, microbial and fungal ecologists typically test the importance of environmental variables on fungal diversity at the level of orders, classes or phyla, but not their subranks or various ranks intermixed due to simplicity and avoiding confusion (e.g. Tedersoo et al.

2014; Maestre et al. 2015). For better comparability across fungi and preferably across all organisms, taxonomic ranks should be monophyletic and exhibit at least roughly similar age (Hennig 1966; Avise and John 1999; Yilmaz et al. 2014; Samarakoon et al. 2016; Hyde et al. 2017; Tedersoo 2017a). For example, orders and classes in chytrids and zygomycetes should ideally correspond to these ranks in Dikarya. So far, the class rank is little used and orders are non-corresponding in most early-diverging lineages such as Chytridiomyceta, Rozellomyceta, Zoopagomyceta, etc. This is due to great differences in the described richness, an order of magnitude different number of taxonomists working on these groups and the abundance of phylogenetically informative morphological and ecophysiological characters (Samarakoon et al. 2016). A number of reclassifications have been performed in Pucciniomycotina and Agaricomycotina to make the constituent orders and classes correspond to those in Ascomycota (Doweld 2001; Bauer et al. 2006). Using divergence time in ranking taxa has recently gained popularity in mycology, but these studies focus on specific phyla, classes or lower-level taxa (Hongsanan et al. 2017; Liu et al. 2016; Zhao et al. 2016, 2017; Hyde et al. 2017).

Although plant and fungal taxonomists follow the criterion of monophyly (i.e. taxa share an exclusive common ancestor), this is commonly violated in higher-level classification of eukaryotes (including fungal phyla) as many of the high-ranking taxa are intentionally maintained poly- or paraphyletic (such as Choanozoa in Fig. 1; e.g. Cavalier-Smith 2013; Ruggiero et al. 2015). Because of different resolution and poor correspondence of ranks among phyla in terms of evolutionary time, the modern fungal classification systems of Species Fungorum (www.speciesfungorum.org), MycoBank (www.mycobank.org), UNITE (Abarenkov et al. 2010), Faces of Fungi (Jayasiri et al. 2015), International Nucleotide Sequence Databases consortium (<https://www.ncbi.nlm.nih.gov/taxonomy>), Adl et al. (2012), Cavalier-Smith et al. (2014) and Ruggiero et al. (2015) do not fully satisfy the expectations of ecologists and biodiversity researchers.

The objective of this initiative is to develop the fungal classification as a user-friendly tool for both taxonomists and ecologists. We propose an updated higher-level classification scheme for the Fungi and a backbone classification tree that accounts for published phylogenies, divergence times and monophyly criterion. We also present a bioinformatics routine that can be utilized in evolutionary ecological studies using any classification scheme and organism group. To demonstrate its usefulness in addressing complementary research questions, we provide an example about testing evolutionary hypotheses in a global ITS-based high-throughput sequencing data set.

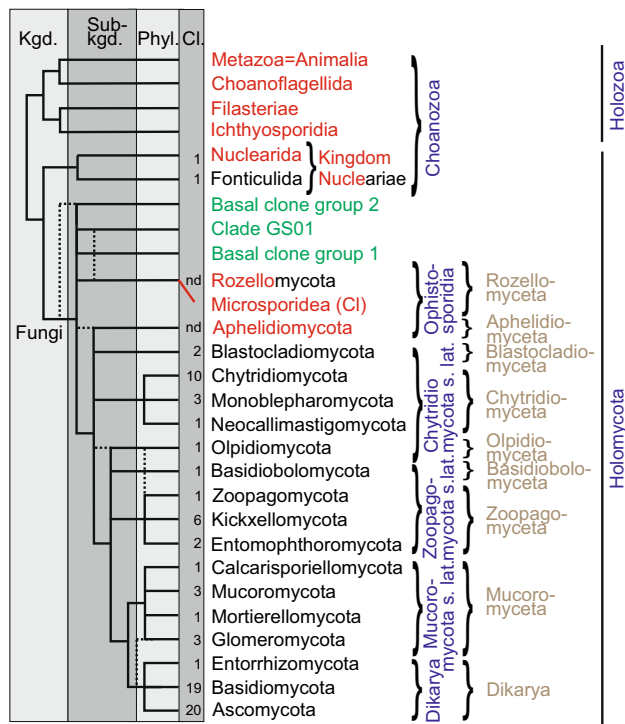


Fig. 1 Updated phylum-level classification of fungi. Numbers behind branches indicate the number of classes included. Names in red indicate taxa traditionally considered under the Zoological nomenclature; names in green indicate unofficial names of undescribed major clades; names in blue indicate old classification and taxonomic super- and subranks. Names in brown depict names of taxa corresponding to subkingdom rank. Phylogenies are compiled from James et al. (2006a), Jiang et al. (2011), Parfrey et al. (2011); Cavalier-Smith et al. (2014); Lazarus and James (2015), Torruella et al. (2015), Spatafora et al. (2016) and Tedersoo et al. (2017). The numbers of classes are adapted from the proposed taxonomy (Online Resource 2). The ages of kingdoms and phyla exceed 1000 and 542 Ma, respectively (Table 1)

Methods

Revised classification of Fungi within eukaryotes

To provide independent estimates of phylogenetic relationships and divergence times within Holomycota, we constructed dated phylogenies based on 18S and 28S rRNA gene sequences. Initially, we selected 111 taxa (at least two taxa from each phylum) to represent multiple classes from all fungal phyla, Nucleariida, Fonticulida as well as Metazoa and Choanoflagellida (outgroups). Sequences were aligned using MAFFT (<https://mafft.cbrc.jp/alignment/server/>), followed by manual editing and exclusion of unambiguously aligned regions. Maximum Likelihood (ML) phylogenies were constructed using RAxML 8.2.10 (Stamatakis 2014) over CIPRES Science Gateway platform (<https://www.phylo.org/>). Members of Microsporidea, clade GS01 and other taxa with branch length exceeding

the average > 3-fold were removed from the alignment, because these destabilized the phylogeny via long branch attraction (available as Online Resource 1). The final data set was comprised of 90 terminals and 5296 characters, which was subjected to ML analysis with 1000 bootstrap replicates and molecular clock analysis using BEAST v2.4. (Bouckaert et al. 2014). To compare the phylogenetic congruence among phyla, we also used alignments of James et al. (2006a) for RNA Polymerase II subunits 1 (RPB1) and 2 (RPB2) and Translation Elongation Factor 1 α (TEF1 α), supplemented with more recent sequences from the early branching fungal lineages. Because < 50% of terminal taxa and phyla were shared among rRNA and protein-encoding genes, it was unfeasible to run a combined analysis.

For the molecular dating analysis, we used a secondary calibration point for the Holomycota clade because of excluding protists. We used four other fossil-based calibration points, which also included the parent node (i.e. stem age) of each clade ('use originate' option). As the calibration prior for the Holomycota, we applied a log-normal distribution with a mean in real space of 200, a standard deviation of 0.3, and an offset of 885 Ma. The offset is based on minimum inferred data for this node (Berbee and Taylor 2001), and the distribution was set to accommodate for other inferred dates (Table 1), which averaged 1028.7 Ma. For the fossil-based calibrations, we set the minimum age of Ascomycota to 440 Ma (*Ornatifilum*), Glomeromycota to 410 Ma (*Scutellosporites devonicus*), Blastocladiomycota to 410 Ma (*Palaeoblastocladiella milleri*) and Basidiomycota to 330 Ma (hyphae with clamp connections) following Taylor et al. (2014), and applied a lognormal prior distribution in real space for each (mean = 200, sd = 0.1). Except for the calibrated nodes, no other clade was constrained to be monophyletic. Both rRNA gene partitions were linked to infer a topology and branch lengths jointly, but for clock and substitution models, partitions were left unlinked. The substitution model was inferred together with the phylogeny by using the BEAST 2 package bModelTest (Bouckaert and Drummond 2017). Model parameters were averaged over visited substitution models and weighted given the support of each model. We used a lognormally distributed relaxed clock model with default priors (uclMean = Uniform [-inf,inf]; uclStddev = Gamma[0,inf]) to account for branch-rate heterogeneity. Two MCMC chains were run in parallel for 170 million generations, sampling every 20,000 states. Convergence and chain mixing were assessed by visually inspecting and comparing log files in Tracer v1.6 (Rambaut et al. 2014). After a burnin of the first 10% of states, posterior estimates were summarized onto a maximum-clade-credibility (MCC) tree using TreeAnnotator from the BEAST 2 suite. Posterior stem ages for all groups

Table 1 Estimates of divergence times for Holomycota and fungal higher taxa

Taxon	Redecker et al. (2000) (18S)	Berbee and Taylor (2001) (18S)	Berney and Pawlowski (2006) (18S)	Taylor and Berbee (2006) (18S)	Lücking et al. (2009) (unkn.) ^a	Gueidan et al. (2011) (5 genes)	Parfrey et al. (2011) (scen. e, g; 16 genes)	Floudas et al. (2012) (scen. 1; 26 genes)	Gaya et al. (2015) (4 genes)	Chang et al. (2015) (136 genes)	This study (18S + 28S)
Difference/kurtosis ^b	0.88/–	0.85/1.05	1.02/0.87	1.13/0.80	1.03/1.05	0.95/0.92	1.22/1.11	1.05/1.10	0.92/1.05	0.98/1.03	0.93/1.17
Holomycota		885	960	1040	1090	966	1240		1020		1108
			(797–1165)		(860–1170)	(875–1061)			(945–1125)		(979–1379)
Fungi											1042
Fungi (crown)		830 ^c	800 ^c		830	775	1040		710	888	966
					(590–1020) ^c	(673–883)			(640–780) ^c	(779–1103)	(672–1259)
Rozellomycota						775				888	966
						(673–883)				(779–1103)	(807–1173)
Blastocladiomycota		775				730	960		710	794	858
						(630–835)	(870–1080)		(640–780)	(762–835)	(408–1078)
Chytridiomyceta		655	800			705	1040	812	670	752	624
						(620–800)	(930–1160)	(622–1043)	(620–720)	(750–764)	(556–724)
Chytridiomycota		< 655	660							636	538
										(561–697)	(195–670)
Monoblepharomycota			660							636	538
										(561–697)	(195–670)
Neocallimastigomycota										676	570
										(610–724)	(249–683)
Zoopagomyceta		800				670			630	699	763
						(600–750)			(570–685)	(654–735)	(504–924)
Entomophthoromycota		775								586	724
										(476–672)	(476–924)
Kickxellomycota		< 800								586	684
										(476–672)	(440–886)
Mucoromyceta				790		630	860	770	610	664	789
						(565–695)	(780–980)	(600–978)	(550–665)	(617–704)	(642–940)
Mortierellomycota										511	727
										(402–596)	(614–867)
Glomeromycota	610	590	725		720	510			520	511	642
					(690–730)	(405–615)			(445–595)	(402–596)	(597–720)
Mucoromycota		610				510			520	578	626
						(405–615)			(445–595)	(489–651)	(264–782)
Mucoromycota (crown)						> 430			> 420	262	560
									(330–480)	(172–352)	(183–735)
Dikarya	610	610	725	790	720	630	860	770	610	664	642
					(690–730)	(565–695)	(780–980)	(600–978)	(550–665)	(617–704)	(597–720)

Table 1 (continued)

Taxon	Redecker et al. (2000) (18S)	Berbee and Taylor (2001) (18S)	Berney and Pawłowski (2006) (18S)	Taylor and Berbee (2006) (18S)	Lücking et al. (2009) (unkn.) ^a	Gueidan et al. (2011) (5 genes)	Parfrey et al. (2011) (scen. e, g; 16 genes)	Floudas et al. (2012) (scen. 1; 26 genes)	Gaya et al. (2015) (4 genes)	Chang et al. (2015) (136 genes)	This study (18S + 28S)
Ascomycota	555	550	600	720	670 (500–800)	583 (506–662)	730 (640–850)	662 (520–831)	545 (500–590)	596 (544–646)	606 (566–661)
Ascomycota (crown)		430	560	660	529 (305–630)	538 (462–612)	570 (480–660)	518 (403–665)	495 (450–540)	510 (454–570)	483 (253–600)
Basidiomycota	555	550	600	720	670 (500–800)	583 (506–662)	730 (640–850)	662 (520–831)	545 (500–590)	596 (544–646)	533 (476–597)
Basidiomycota (crown)		490	350	550		450	510 (410–630)	521 (480–536)	435 (375–500)	473 (402–539)	445 (268–551)

Values indicate average estimates and 95% CI (in parenthesis, if given) for stem ages

^aRange of estimates given in parentheses

^bDifference, proportional deviation on mean estimates for average divergence times of Holomycota, Chytridiomycota, Dikarya and Ascomycota crown; kurtosis, ratio of mean deviation of Holomycota to Ascomycota crown (or Chytridiomycota to Ascomycota crown), with larger values indicating relatively greater phylogenetic distance between these groups

^cNo Rozellomycota included, indicating underestimates

were extracted by importing post-burnin posterior tree to R v3.4 (R Core Team 2017), using functions in *ape* (Paradis et al. 2004) and *phangorn* (Schliep 2011) packages.

To update fungal classification, we systematically compiled taxonomic literature concerning order to phylum level molecular phylogenies of fungi and other major groups of eukaryotes. This information was compared with the current classification of Fungi using multiple sources (Adl et al. 2012; Cavalier-Smith 2013; Ruggiero et al. 2015; Species Fungorum, International Nucleotide Sequence Databases consortium, MycoBank and UNITE as of 12 October 2017. We used the following principles for taxonomic hypotheses: (1) taxa should be monophyletic based on molecular phylogenies; and (2) the basic taxonomic ranks should reflect divergence times. We selected 542 Ma (the Phanerozoic-Proterozoic boundary) of divergence to separate class and subphylum vs. phylum-level treatment of Dikarya, zygomycetes and ‘chytrids’, which corresponds to the original proposal of Hennig (1966) for animals and matches the recommended time line for Ascomycota (Hyde et al. 2017). Groups with divergence times over roughly 700 Ma were treated in different subkingdoms. To reduce the potential analytical bias of this study, we considered mean divergence time estimates across multiple independent estimates (Table 1).

We found that the classification provided in International Nucleotide Sequence Databases consortium is by far the most updated regarding current taxonomic literature and thus, we used this as a baseline for proposed corrections. We also accommodated previously unrecognized soil fungal clades (cf. Tedersoo et al. 2017) to this classification (Online Resource 2), because many of these groups are common and diverse in the soil environment and there are no available reference sequences from formally described species.

Evolutionary ecological analysis tool

To enable evolutionary ecological analyses, we converted the proposed hierarchical classification to newick format to serve as input to Phylocom (<http://phylodiversity.net/phylocom/>), picante (Kembel et al. 2010) and S.PhyloMaker (Qian and Jin 2016) packages of R using the perl script taxonomy_to_tree.pl (Online Resource 3). For each nine taxonomic ranks (species, genus, family, order, class, subphylum, phylum, subkingdom and kingdom), we used the default branch length = 60 that can be easily divided into full numbers. The branch length of each rank and each taxon can be modified by custom preferences to account for subranks and different age of taxa. The full taxonomic table with branch length parameters in separate columns represent the input for classification tree. A newick-formatted tree with branch length information represents the output (Fig. 2). The respective backbone tree of fungi,

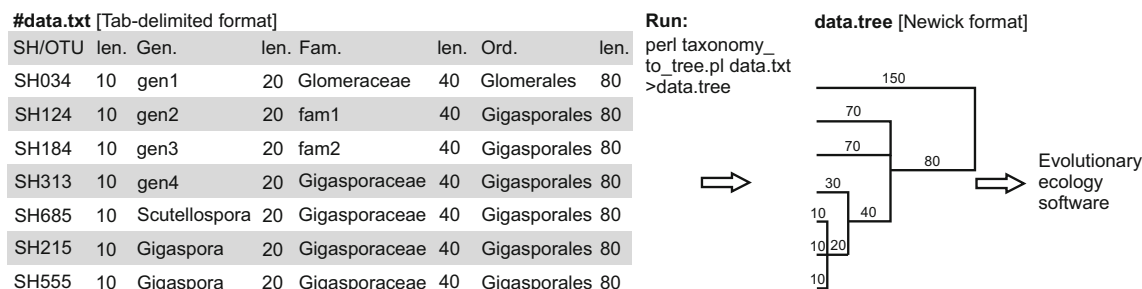


Fig. 2 Outline of the workflow and input and output of the evolutionary ecological analysis tool taxonomy_to_tree.pl. This example indicates assignment of exponentially increasing weight to

higher-level relationships. Compatible software includes picante and S.PhyloMaker packages of R and Phylocom

Fungi_TH_1.1, is given in Online Resource 4. The same perl script can be used to assign fungal Species Hypotheses (cf. Kõljalg et al. 2013) or OTUs of any taxon to custom classification trees based on a combination of their accessions and taxonomic profile from species to higher ranks. The updated classification table of fungi and other eukaryotes is available in FAIR data format as Online Resource 2 (Tedersoo 2017b).

To test the performance of the phylogenetic tool, we utilized the global soil fungal data set of 313 high-quality samples by 44,571 OTUs (Tedersoo et al. 2014). We sought to test the hypothesis that OTU-level taxonomic richness, phylogenetic diversity and phylogenetic overdispersion of fungi exhibit similar patterns across biomes. The initial fungal and unassigned OTUs were re-classified based on the updated classification and assigned to the classification backbone with branch length = 60 between each of the eight ranks. For each sample, we calculated the phylogenetic diversity (total branch length for all OTUs per sample) and uniqueness (unique branch length for each sample) metrics (cf. Lozupone et al. 2007) as well as the nearest taxon index (NTI) and net relatedness index (NRI). NTI and NRI depict phylogenetic overdispersion (negative values) and phylogenetic clustering (positive values) across the sister OTUs and across the entire phylogenetic tree, respectively (Webb 2000). We used the number of OTUs to weigh the phylogenetic diversity (PD_{OTU}) and uniqueness metrics (UNI_{OTU}), because of their strong initial correlation ($R > 0.7$) with richness. We calculated standardized residuals for OTU richness, accounting for square-root function of sequencing depth. We also attempted to compile a community phylogenetic dissimilarity matrix using UNIFRAC distance, but this computation-intensive process was not completed within one week. We tested the effect of biomes and tree vs. grass-dominated (grasslands, savannas, low tundra) habitats on the five richness and diversity metrics using one-way ANOVAs supplied with Tukey HSD tests for unequal sample size. None of the metrics were correlated with sequencing depth or residuals of the number of OTUs ($R < 0.17$).

Results and discussion

Phylogenetic relationships in Holomycota including Fungi

Phylogenetic analyses of nearly complete rRNA genes provided strong resolution for the order of divergence for most fungal phyla and provided estimates of their divergence times, which were roughly in agreement with previous rRNA-based analyses, but provided relatively greater support values due to more inclusive taxon sampling covering uncultured groups (Figs. 3, 4). The phylograms of RPB1 and RPB2 genes were generally congruent with rRNA gene concerning the placement of the major fungal groups, with the exception of the position of Glomeromycota and Mortierellomycota (Figs. 5, 6). Contrasting positions of these groups are also evident in previous multigene and phylogenomic studies (James et al. 2006a; Spatafora et al. 2016). Differences in placement of other groups are almost certainly affected by the paucity of protein-encoding gene data for many critical taxa (e.g. the early diverging lineages, *Entorrhiza*, *Calcarisporiella*, *Olpidium*). The TEF1 α marker did not reveal any strong relationships among phyla (not shown).

Consistent with most other rRNA-based (Brown et al. 2009) and phylogenomics (Torruella et al. 2015) studies, the amoeboid protist orders Nucleariida and Fonticulida constituted a strongly supported sister taxon to Fungi (Figs. 3, 4). The soil- and freshwater-inhabiting Basal Clone Group 2 (BCG2; Monchy et al. 2011) formed a well-supported sister lineage to the rest of the Fungi (Figs. 3, 4). In a more inclusive taxon sampling, BCG2 was related to the terrestrial clade GS01 (Tedersoo et al. 2017), which grouped with Microsporidea within Rozellomycota, probably due to long branch attraction, in this study (Online Resource 1). Another formally undescribed phylum-level group, the marine Basal Clone Group 1 (BCG1; Nagahama et al. 2011) was placed as a sister group of Rozellomycota (Figs. 3, 4) in our analyses, although with moderate

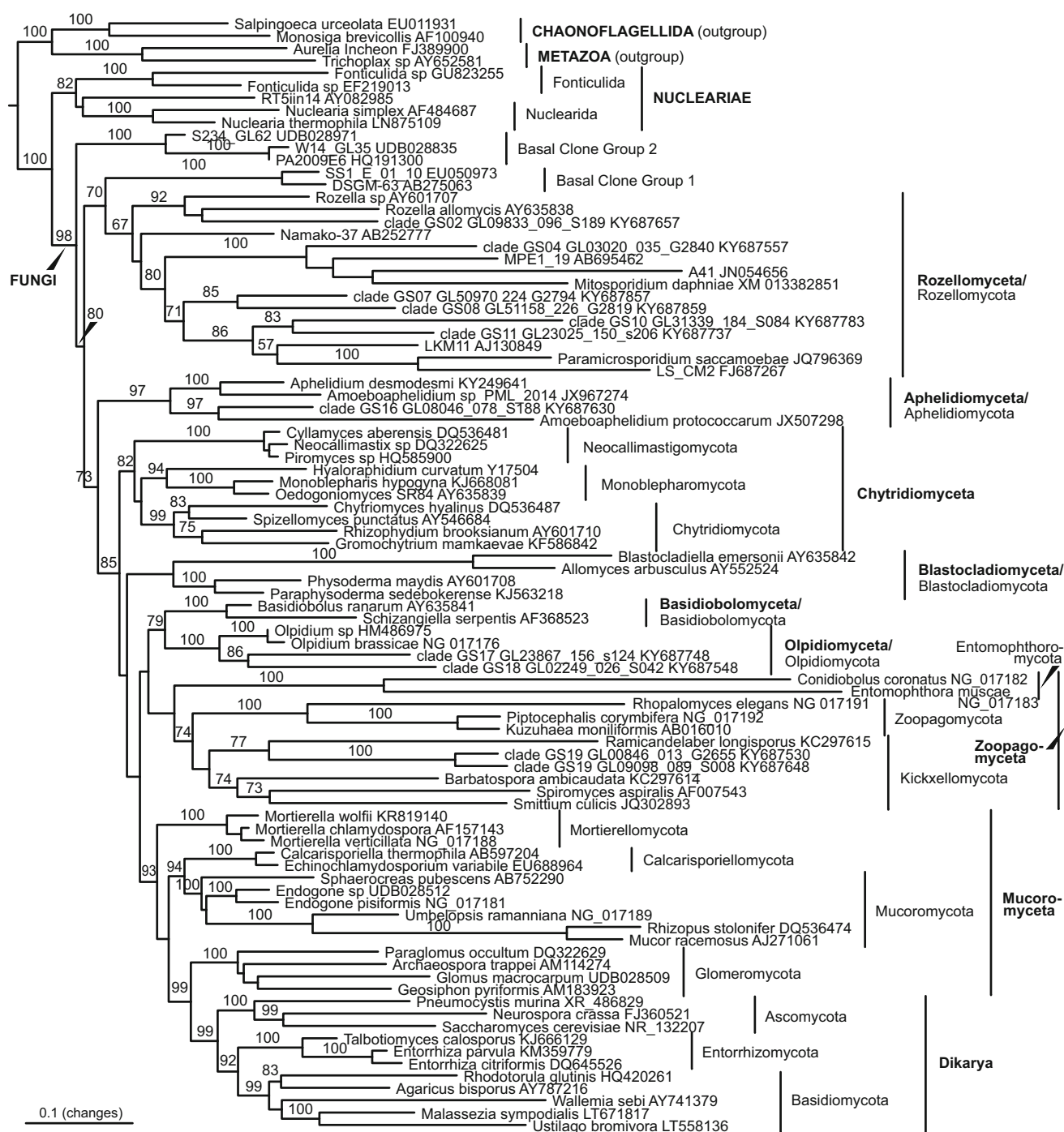


Fig. 3 Maximum Likelihood phylogram of Holomycota with rapid bootstrap support values above branches (values > 60 shown)

support. Understanding phylogenetic affinities of the uncultured clades GS01 and BCG1 certainly requires analysis of more genes.

The aphelids branched off after the clades of BCG2 and Rozellomycota + BCG1, with strong support. This pattern supports previous rRNA gene-based studies (Tedersoo et al. 2017), but conflicts with some other analyses utilizing rRNA (Karpov et al. 2017b; Letcher et al. 2017) or protein-

encoding (Torruella et al. 2017) genes. These studies that may suffer from lower taxon sampling, place aphelids close to Rozellomycota.

The branching order of ‘chytrids’ and zoopagaceous zygomycetes was poorly resolved, but most of the phyla were strongly supported as monophyletic (Figs. 3, 4). Multigene and phylogenomics studies also provide conflicting information about the divergence order of these

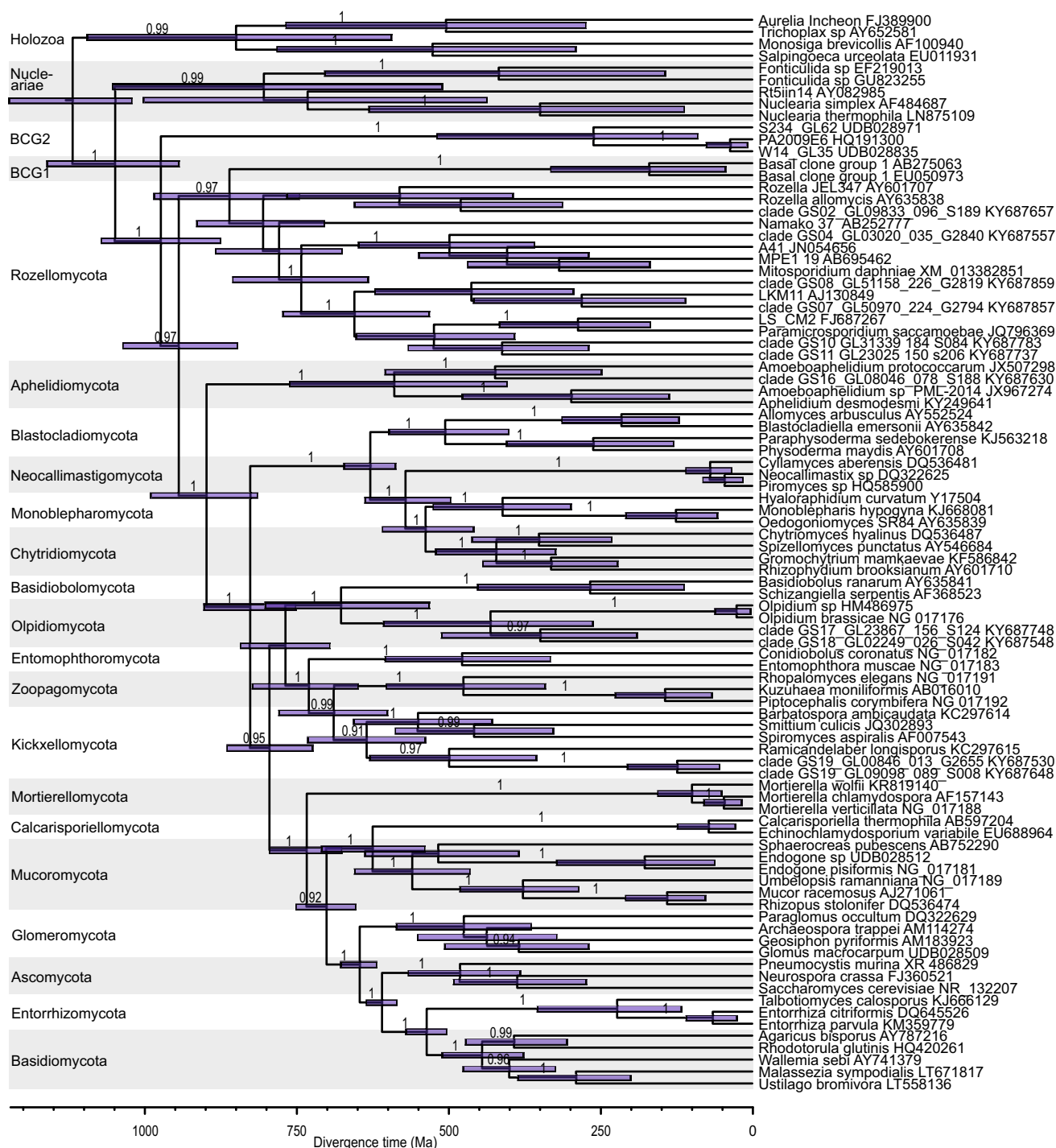


Fig. 4 Bayesian phylogram of Holomycota indicating divergence time estimates (median; bars, 95% CI; bars for many unsupported clades not shown). Values above branches indicate Bayesian posterior probabilities (values < 0.90 not shown)

groups (James et al. 2006a; Spatafora et al. 2016). Nonetheless, these studies are in agreement with our analyses in maintaining the mucoromycetous zygomycetes and Dikarya, taken together, monophyletic. Yet, while multigene studies keep the mucoromycete zygomycetes

monophyletic, these groups branch off separately in our rRNA-based phylograms. This is known to be one of the greatest disparities of rRNA and most protein-encoding genes in settling higher-level fungal evolution (Spatafora et al. 2016).

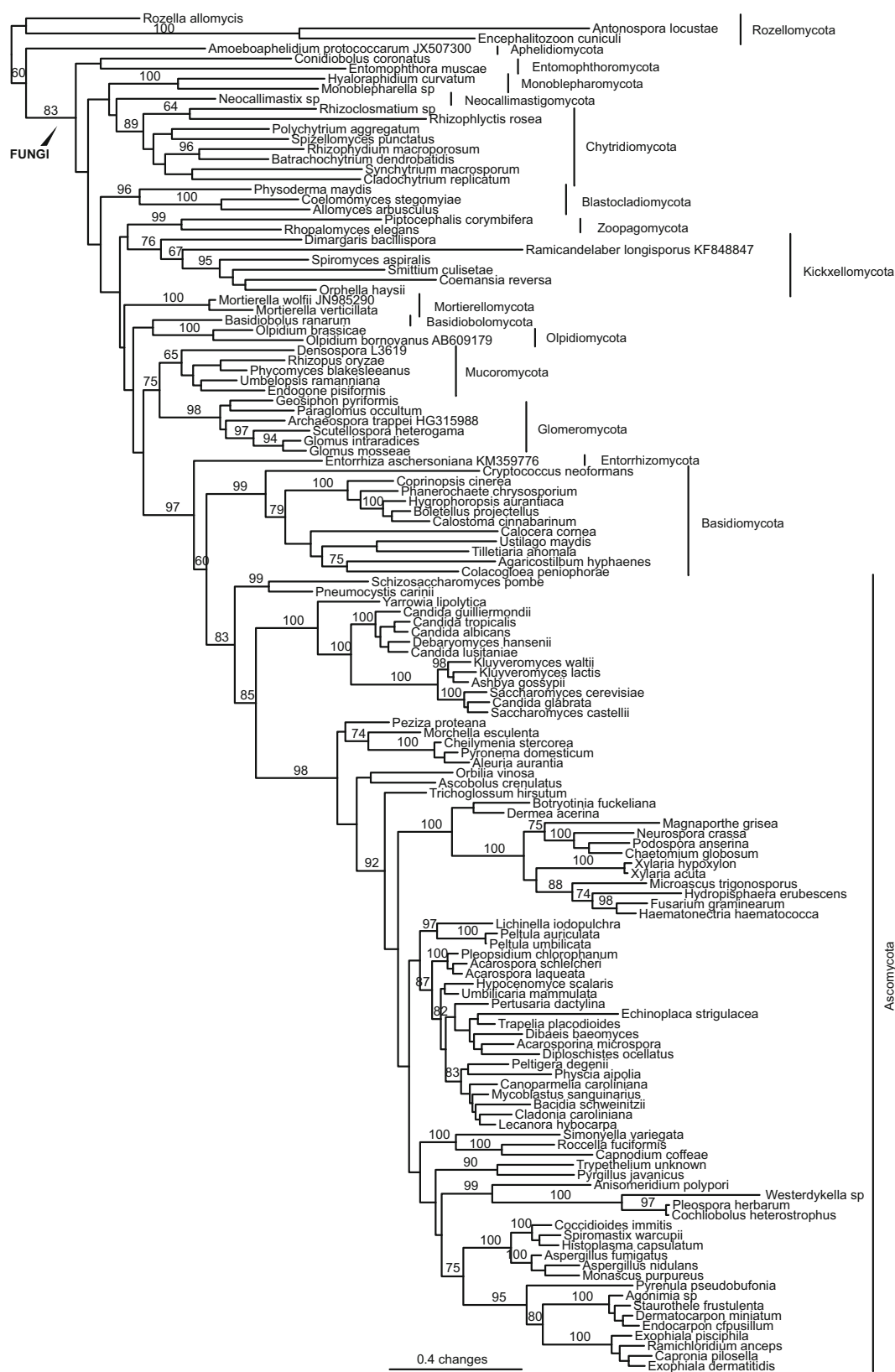


Fig. 5 Maximum Likelihood RPB1 tree of Fungi based on amino acid alignment. The alignment contains 135 taxa and 1085 positions. Bootstrap support > 60 is indicated above branches. Accessions are given for terminals not included in James et al. (2006a)

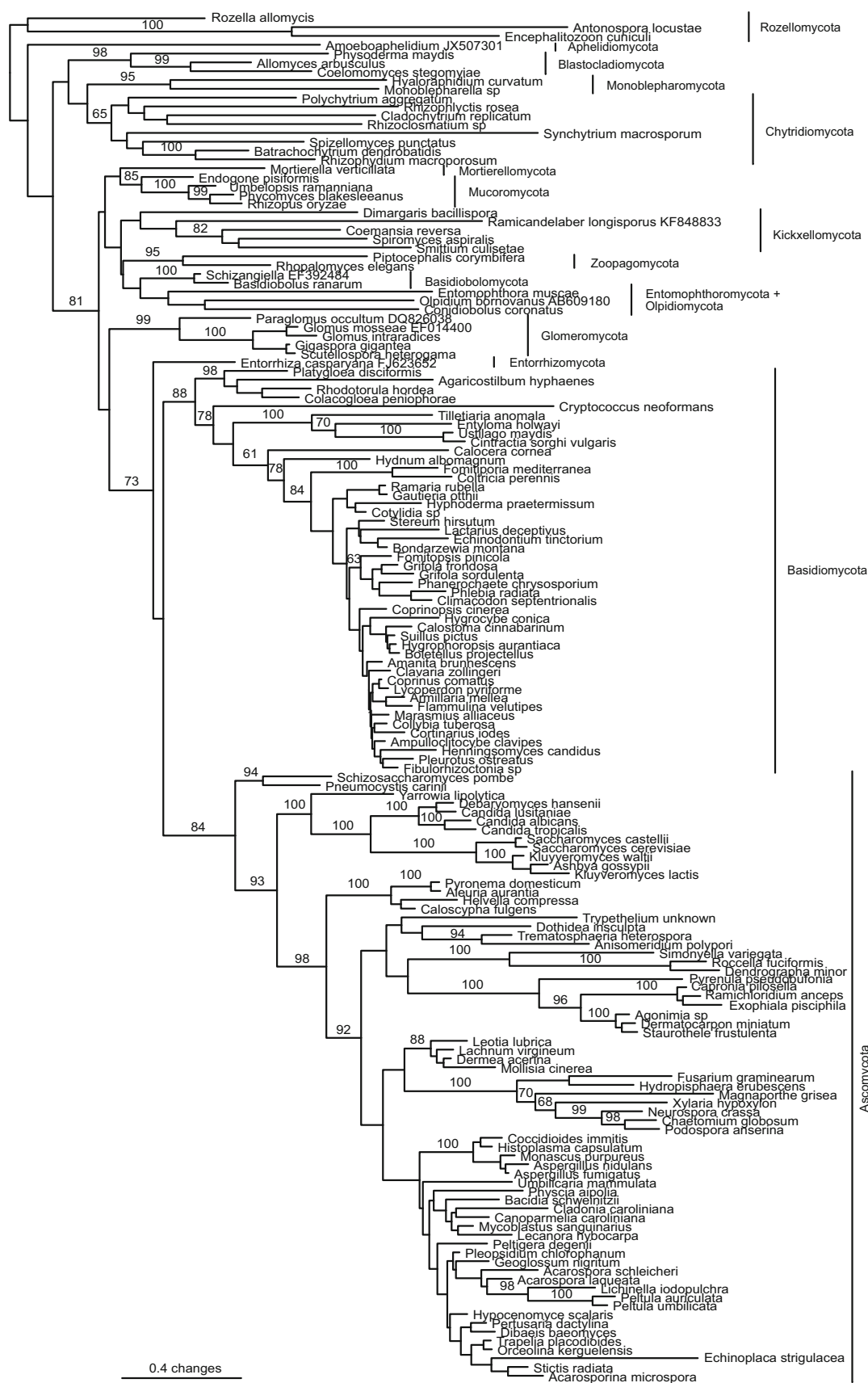


Fig. 6 Maximum Likelihood RPB2 tree of Fungi based on amino acid alignment. The alignment contains 152 taxa and 987 positions. Bootstrap support > 60 is indicated above branches. Accessions are given for terminals not included in James et al. (2006a)

Updated classification of Holomycota including Fungi

Combining molecular phylogenies and molecular clock-based divergence time estimates of this and previous studies (Table 1) enabled to account for extreme and potentially erroneous values of individual analyses and collectively provided a strong basis for age-based higher-level fungal classification. Based on divergence time estimates of this and other eukaryote-wide studies (Samarakoon et al. 2016; Tedersoo 2017a), we established the critical ages of ca 1000 Ma, ca 700 Ma and 542 Ma (the Phanerozoic-Proterozoic boundary) as minimum ages for kingdoms, subkingdoms and phyla, respectively.

We estimated the divergence time between Fungi and Nucleariida-Fonticulida at 1042 Ma and the latter group radiated further 816 Ma (mean ages). Nucleariida and Fonticulida are collectively known as Cristidiscoidea hinting to the discoid mitochondrial crista, a feature shared with some groups of Cercozoa (Page, 1987; Scoble and Cavalier-Smith 2014). Berbee et al. (2017) proposed to include Nucleariida and Fonticulida within the extended kingdom Fungi. This is not, however, warranted in our opinion, because these taxa have never been considered as Fungi and the constituent taxa have several unique structural (lack of chitin cell walls, discoid mitochondrial cristae) and ecophysiological (amoeboid habit, phagocytotic nutrition) characters as well as specific features in genomic structure such as the lack of division II Chitin synthase gene (James and Berbee 2012; Torruella et al. 2015). Because *Nuclearia* spp. and *Fonticula alba* form deep lineages in a sister position to Fungi (Figs. 3, 4, Online Resource 1) and they possess different lifestyles as single and colonial amoebae, respectively, we advocate that both groups warrant a phylum of their own within the kingdom Nucleariiae. Based on the type genera *Nuclearia* and *Fonticula*, we propose phyla Nucleariida and Fonticulida, respectively. Recent studies indicate that Nucleariiae are phylogenetically diverse and perhaps more common in aquatic habitats than soil (López-Escardó et al. 2018).

Within the kingdom Fungi, we follow the current International Nucleotide Sequence Databases consortium taxonomy as much as feasible based on the examination of phylogenies and classifications. We propose several changes at the phylum and class level and we further introduce subkingdoms to enable communication of related phyla. Of the nine subkingdoms, Dikarya (Basidiomycota,

Ascomycota and Entorrhizomycota), Mucoromyceta (Calcarisporiellomycota, Glomeromycota, Mortierellomycota and Mucoromycota), Zoopagomyceta (Entomophthoromycota, Kickxellomycota, Zoopagomycota) and Chytridiomyceta (Chytridiomycota, Monoblepharomycota, Neocallimastigomycota) comprise multiple phyla, whereas Aphelidiomyceta, Basidiobolomyceta, Blastocladiomyceta, Olpidiomyceta, Rozellomyceta cover a single phylum. We propose raising eight taxa from lower taxonomic levels to phylum rank—i.e., Basidiobolomycota, Calcarisporiellomycota, Glomeromycota, Entomophthoromycota, Kickxellomycota, Monoblepharomycota, Mortierellomycota and Olpidiomycota—to follow the criteria of monophyly and comparable divergence time (Figs. 3, 4; Table 1). These distinctions are also supported by key ecophysiological differences among these groups (Spatafora et al. 2017). Many of the phyla have been described previously, but have not been adequately classified.

Multiple unicellular groups of organisms occur at the base of fungal tree of life and their position within or outside fungal kingdom is debatable. The clades GS01 and Basal Clone Group 2 represent a potential successive sister lineage to all fungal phyla, albeit with limited statistical support (Tedersoo et al. 2017, 2018). Since nothing is known about the morphology of these clades, we consider these tentatively as subkingdom-level groups within Fungi, because of their supported monophyly with Fungi and divergence time of < 1000 Ma. Many taxonomists place the unicellular Rozellomycota, Microsporidia and Aphelida within Fungi (James et al. 2006a; Jones et al. 2011a, Adl et al. 2012; James and Berbee 2012 and further studies on fungal classification), but other authors indicate the monophyly of Aphelida and Rozellomycota in a sister position to all other Fungi (Karpov et al. 2013; 2014b, 2017b; Letcher et al. 2013, 2017) and treat this so-called ARM clade as phylum Ophisthospordia (Karpov et al. 2014b) or a part of the intentionally paraphyletic phylum Choanozoa, which includes protists at the base of Metazoa (Cavalier-Smith 2013; Ruggiero et al. 2015). However, taxonomically more inclusive phylogenies place these groups separately—Rozellomycota and Microsporidia at the basal position of Fungi but Aphelida nested within ‘chytrids’ and/or zoopagaceous zygomycetes (Lazarus and James 2015; Tedersoo et al. 2017, 2018). Therefore, we suggest renaming of Aphelida to Aphelidiomycota to meet the standards of nomenclature. We prefer the name Rozellomycota over Cryptomycota, because (1) the phylum-level taxon Rozellida was described before Cryptomycota and (2) Rozellida hints to the type *Rozella*, whereas Cryptomycota hints to *Cryptomyces*, which is an ascomycete. Recent phylogenies indicate that Microsporidia are deeply nested within Rozellomycota (Corsaro et al. 2014; Haag et al. 2014; Keeling et al. 2014; Tedersoo

et al. 2017). To keep Rozellomycota a single monophyletic phylum, we consider microsporidians at the class (Microsporidea) level within this group. Because of the historical taxonomic ‘heritage’, classification of Microsporidea needs to follow the International Code of Zoological Nomenclature (see Didier et al. 2014). Rozellomycota and other fungal phyla share the division II Chitin synthase gene, which is absent in the Nucleariæ (James and Berbee 2012). Furthermore, Rozellomycota and other fungal phyla share the AAA lysine synthesis pathway and predominately osmotrophic nutrition (Corsaro et al. 2014). Chitin is present in cell wall of all fungal groups including some life stages of Microsporidea, but it has been apparently secondarily lost in many if not all members of Rozellomycota due to their endoparasitic lifestyle (Jones et al. 2011b; Corsaro et al. 2014). Unfortunately, much less is known about the structure and genome of Aphelidiomycota, but existing evidence points to their great similarity to Rozellomycota (Karpov et al. 2014b, 2017b). Most importantly, much of the scientific community has accepted Rozellomycota as part of fungi (evident in continuously evolving classification systems of International Nucleotide Sequence Databases consortium, UNITE, MycoBank).

Within the former ‘chytrid’ group, Monoblepharomycota is considered as a separate phylum comprising classes Hyaloraphidiomycetes, Monoblepharidomycetes and Sanchytriomycetes *class nov.*, following the phylogenies in Powell and Letcher (2014) and Karpov et al. (2017a). The treatment of the family Olpidiaceae within Olpidiomycota at the phylum level is warranted based on phylogenies and age, but its exact position remains uncertain (James et al. 2006a; White et al. 2006; Sekimoto et al. 2011). Although Basidiobolomycetes is treated within Entomophthoromycota (Humber 2012), these associations are not supported by individual genes (Figs. 3, 4, 5; Sekimoto et al. 2011; Gryganskyi et al. 2013) and therefore, we consider this taxon as a separate phylum. Our rRNA and RPB1 gene analyses revealed a moderately supported sister relationship between Basidiobolomycota and Olpidiomycota (mean estimated divergence, 682 Ma) supporting an earlier hypothesis of James et al. (2006a).

The formerly known phyla Mucoromycota and Zoopagomycota are emended so that these are comprised of the subphylum Mucoromycotina and Zoopagomycotina, respectively (sensu Spatafora et al. 2016). Entomophthoromycota comprise the subphylum Entomophthoromycotina with the classes Entomophthoromycetes and Neozygitomycetes (Humber 2012). The subphylum Kickxellomycotina is treated at phylum rank (Kickxellomycota), whereas its constituent orders and deeply branching orphan genera are raised to class rank (Asellariomycetes, Barbatosporomycetes, Dimargaritomycetes, Harpellomycetes, Kickxellomycetes; Ramicandelaberomycetes)

based on a multi-gene phylogenetic treatment (Tretter et al. 2014).

The newly described Calcarisporiellomycota *phylum nov.* (comprising *Calcarisporiella thermophila* and *Echinochlamydosporium variabile*) represents a deep lineage with strongest affinities to Mucoromycota (Hirose et al. 2012; Yamamoto et al. 2015) or Mortierellomycota (Jiang et al. 2011; Tedersoo et al. 2017). Mortierellomycota is treated as a distinct phylum because of consistent phylogenetic distinction of Mortierellales from the remaining Mucoromycota (James et al. 2006a; Sekimoto et al. 2011; Spatafora et al. 2016; Tedersoo et al. 2017). We also accept Glomeromycota at the phylum rank as initially proposed by Schüßler et al. (2001), rather than take up subphylum Glomeromycotina as proposed by Spatafora et al. (2016). We find that its deep divergence within Mucoromycota warrants a phylum-level distinction, which is supported by its asexual habit and exclusively arbuscular mycorrhizal lifestyle, which also occurs in Endogonomycetes of Mucoromycota (Orchard et al. 2017). Following Oehl et al. (2011), the orders of Glomeromycota are treated at the class rank, viz. Archaeosporomycetes, Glomeromycetes (comprising Diversisporales, Gigasporales and Glomerales) and Paraglomeromycetes, with mean divergence times at 384–477 Ma (Fig. 4). Although our rRNA gene analyses suggest that Mucoromycota are paraphyletic with respect to Dikarya, protein-encoding genes (including RPB1; Fig. 5) provide strong support for the monophyly Mycoromycota as a sister group to Dikarya (Chang et al. 2015; Spatafora et al. 2016). Therefore, we rely on the previous phylogenomics analyses and consider Mucoromycota effectively monophyletic.

At the subphylum and class level, the internal structure of most phyla is retained. Class-level treatment was not attempted for Aphelidiomycota and Rozellomycota due to a lack of formal classification and insufficient sequence data from specimens. We only accommodated the class-level soil fungal clades (cf. Tedersoo et al. 2017) and Microsporidea into the classification system of these phyla. The orders of Mucoromycota are all treated at the class level (Endogonomycetes, Mucoromycetes and Umbelopsidomycetes) due to their deep branching in phylogenies (mean ages 380–560 Ma). Endogonomycetes diverged from other Mucoromycota 560 Ma and radiated 522 Ma (mean ages; Fig. 4), potentially warranting phylum- or subphylum-level consideration, for which more in-depth studies are needed. We also treat all former orders of Chytridiomycota at the class level (mean ages 330–420 Ma), viz. Chytridiomycetes, Cladochytriomycetes, Lobulomycetes, Mesochytriomycetes (comprising Mesochytriales and Gromochytriales), Polychytriomycetes, Rhizophlyctidomycetes, Rhizophydiomycetes, Spizellomycetes and Synchytriomycetes

(James et al. 2006b; Karpov et al. 2014a; Seto et al. 2017; Tedersoo et al. 2017). In the Blastocladiomycota, we accommodate the family Physodermataceae in class Physodermatomycetes, which is warranted by its distinct phytopathogenic mode of nutrition, early branching position and age (505 Ma; James et al. 2006b; Porter et al. 2011). In Zoopagomycota, the order Zoopagales is treated at class rank (Zoopagomycetes). We find that the hierarchy in Ascomycota (Hyde et al. 2017; Wijayawardene et al. 2018) and Basidiomycota (Zhao et al. 2017) has sufficient resolution at the subphylum and class level. Therefore, we only introduce the class Collemopsidiomycetes for the recently described order Collemopsidiales (Perez-Ortega et al. 2016) within Ascomycota.

Proposed nomenclatural changes to the higher-level taxonomy of Holomycota

DIVISION Opisthokonta Cavalier-Smith, Evolutionary Biology of the Fungi:339. 1987

SUPERKINGDOM Holomycota Y. Liu, BMC Evol. Biol. 9:272:3. 2009

= Nucleotmycea M.W. Brown, Mol Biol Evol 26:2706. 2009

KINGDOM Fungi R.H. Whittaker, Quart. Rev. Biol. 34:220. 1959

SUBKINGDOM Rozellomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 553988

Diagnosis: Vegetative cells amoeboid, with pseudopodial extensions extending around host organelles; zoospores with a posterior flagellum that has a solid rhizoplast associated with a long kinetosome; one single large mitochondrion (missing in Microsporidea); resting spores thick-walled; chitinous wall present only in some life stages; penetration of host cells via germ tube; intracellular obligate parasites of fungi, animals and protists that consume host organelles via phagocytosis. Type: *Rozella* Cornu

Remark: Corresponds to Rozellomycota Doweld

Phylum Rozellomycota Doweld, Index Fungorum 43:1. 2013

= Rozellida E. Lara, Protist 161:117. 2010; = Cryptomycota M.D.M. Jones & T.A. Richards, IMA Fungus 2:173. 2011; = Rozellomycota D. Corsaro & R. Michel, Parasitol Res 113:1916. 2014; = Rozellomycota T. James & Berbee, Bioessays 34:98. 2011; = Rozellosporidia Karpov, J Euk Microbiol 64:573. 2017

Subphylum Rozellomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554030

Diagnosis: As for subkingdom above. Type: *Rozella* Cornu
Class Microsporidea Corliss & Levine, J. Protozool. 10:26. 1963

Remark: in spite of deep divergence, other subphyla and classes in Rozellomycota are not erected, because of

insufficient knowledge and molecular data from a few fully identified species.

SUBKINGDOM Aphelidiomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 553989

Diagnosis: Phagotrophic amoeboid vegetative stage within a host cell; zoospores produce pseudopodia or have a posteriorly directed functional or rudimentary flagellum; resting spores rounded to oval with a thick smooth cell wall; invasion cyst penetration apparatus with a short infection tube; intracellular parasites of mostly algae. Type: *Aphelidium* (Zopf) Gromov

Remark: Corresponds to Aphelidea Gromov. The above description is combined from Gromov (2000) and Karpov et al. (2014b). Changes in name endings here and below are due to the treatment of the aphelids as Fungi rather than Animalia.

Phylum Aphelidiomycota Tedersoo et al. *phyl. nov.*, Index Fungorum ID: 553990

= Aphelida Karpov, Aleoshin & Mikahilov, Front. Microbiol. 5:112:9. 2014

Diagnosis: As for subkingdom above. Type: *Aphelidium* (Zopf) Gromov

Subphylum Aphelidiomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554031

Diagnosis: As for subkingdom above. Type: *Aphelidium* (Zopf) Gromov

Class Aphelidiomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 553991

= Aphelidea Gromov, Zool. Zh. 79:521. 2000

Diagnosis: As for subkingdom above. Type: *Aphelidium* (Zopf) Gromov

Order Aphelidiales Tedersoo et al. *ord. nov.*, Index Fungorum ID: 553992

= Aphelidida Gromov, Zool. Zh. 79:521. 2000

Diagnosis: As for subkingdom above. Type: *Aphelidium* (Zopf) Gromov

Family Aphelidiaceae Tedersoo et al. *fam. nov.*, Index Fungorum ID: 553993

= Aphelididae Gromov, Zool. Zh. 79:521. 2000

Diagnosis: As for subkingdom above. Type: *Aphelidium* (Zopf) Gromov

SUBKINGDOM Blastocladiomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 553994

Diagnosis: Thallus monocentric or polycentric, may form hyphae; zoospore with a single flagellum that lacks electron-opaque plug in transition zone; cone-shaped nucleus terminating near the kinetosome; microtubules radiating anteriorly from the proximal end of the kinetosome around the nucleus; sexual reproduction by planogamete fusion (anisogamy); alternant haploid and diploid stages; saprotrophs or parasites on plants, animals and fungi. Type: *Blastocladia* Reinsch

Remark: Corresponds to Blastocladiomycota T. James. The above description is adapted from James et al. (2006b).

Phylum Blastocladiomycota T. James, Mycologia 98:867. 2006

Subphylum Blastocladiomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554032

Diagnosis: As for subkingdom above. Type: *Blastocladia* Reinsch

Class Blastocladiomycetes T. James, Mycologia 98:867. 2006

Class Physodermatomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 553995

Diagnosis: Thallus with rhizoids, endobiotic; dictyosome in sporangium; bipolar germination of zoospores; zoospores with nucleus attached to centriole and nuclear cap of ribosomes; thick-walled, darkly pigmented resting sporangium; sporangium germination by protruding endosporangium; parasites on aboveground tissues of angiosperms. Type: *Physoderma* Wallr.

Order Physodermatales Caval.-Sm., Eur. J. Protist. 49:157. 2012

SUBKINGDOM Chytridiomycota Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 553996

Diagnosis: Thallus monocentric, polycentric or filamentous; zoospores with a single (rarely up to 20) posteriorly-directed flagellum possessing a kinetosome and non-functional centriole, nine flagellar props, and a microbody-lipid globule complex; sexual reproduction with zygotic meiosis; Golgi apparatus with stacked cisternae; nuclear envelope fenestrated at poles during mitosis; saprotrophs or parasites of mostly plants, or commensals in herbivore digestive tract. Type: *Chytridium* A. Braun

Remark: The above description is compiled from Hibbett et al. (2007) and Powell and Letcher (2014).

Phylum Chytridiomycota M. J. Powell, Mycol. Res. 111:513. 2007

Subphylum Chytridiomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554033

Diagnosis: As for subkingdom above. Type: *Chytridium* A. Braun

Class Chytridiomycetes Caval.-Sm., Biol. Rev. 73:246. 1998, *emend.* Tedersoo et al.

Emendation: The class Chytridiomycetes comprises a single order, Chytridiales, following the phylogeny of Powell & Letcher (The Mycota 9a:141–176. 2014). Other orders are assigned to separate classes.

Order Chytridiales Cohn, Jber. Schles. Ges. Vaterl. Kultur 57:279. 1879

Class Cladochytriomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 553997

Diagnosis: Thallus eucarpic, monocentric or polycentric; rhizoids catenulate, isodiametric or tapering. Zoospore chytridioid but with a cord-like microtubular root between

the kinetosome and fenestrated cisterna, composed of up to 25 microtubules interconnected by linkers; a cisterna, microbody, and mitochondrion closely associated with the lipid globule; mostly saprotrophic or pathogenic on algae. Type: *Cladochytrium* Nowak

Remark: The above description is taken from Mozley-Standridge et al. (2009).

Order Cladochytriales S. E. Mozley-Standridge, Mycol. Res. 113:502. 2009

Class Mesochytriomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 553998

Diagnosis: Thallus simple, with inoperculate, monocentric, epibiotic sporangium having endogenous development and slightly branched rhizoids near the sporangial base; zoospore Centriole at an angle of ca. 30° to kinetosome; parasites of freshwater algae. Type *Mesochytrium* B.V. Gromov, Mamkaeva & Pljusch.

Remark: The above description is compiled from Karpov et al. (2014a).

Order Mesochytriales Karpov & Aleoshin, Persoonia 32:124. 2014

Order Gromochytriales Karpov & Aleoshin, Persoonia 32:123. 2014

Class Lobulomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 553999

Diagnosis: Thallus monocentric, eucarpic, with endogenous development; zoospore with opaque flagellar plug, anterior or posterior plug extensions; one or two lipid globules; lacking microtubule root, Golgi apparatus, striated inclusion, and electronopaque bodies near kinetosome; present in soil, dung, marine and freshwater habitats. Type: *Lobulomyces* D.R. Simmons

Remark: The above description is taken from Simmons et al. (2009)

Order Lobulomycetales D. R. Simmons, Mycol. Res. 113:453. 2009

Class Polychytriomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554000

Diagnosis: Thallus polycentric or monocentric; monocentric species with multiple rhizoidal axes. Motile zoospores spherical, usually > 4 µm diam, with or without flagellar plug and kinetosome spur; 0–3 microtubule roots present; nonflagellated centriole equal to or longer than diameter and attached to kinetosome throughout its length; cultures grow on chitin; habitat mostly in soil and freshwater. Type: *Polychytrium* Ajello

Remark: The above description is combined from Longcore and Simmons (2012) and Powell and Letcher (2014).

Order Polychytriales Longcore & D.R. Simmons, Mycologia 104:279. 2012

Class Rhizophlyctidomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554001

Diagnosis: Thallus monocentric, eucarpic; sporangium interbotic, inoperculate or endo-operculate with one or several discharge apparatus, rhizoidal axes multiple; kinetosome at sharp angle to the non-flagellated centriole and attached to it throughout most of the length; cytoplasmic microtubules absent; habitat mostly in agricultural soils. Type: *Rhizophlyctis* Fischer

Remark: The above description is taken from Powell and Letcher (2014).

Order Rhizophlyctidales Letcher, Mycol. Res. 112:1034. 2008

Class Rhizophydiomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554002

Diagnosis: Thallus monocentric; ribosomes enclosed by a system of double membranes; mitochondria, microbodies, lipid globules, and membrane cisterna are typically associated as a microbody-lipid globule complex. The non-flagellated centriole and kinetosome lie parallel or slightly angled toward each other and are connected by fibrillar material. The base of the flagellum proper lacks an electron-opaque plug; parasites and saprobes mostly in soil and freshwater. Type: *Rhizophydium* Schenk

Remark: The above description is combined from Letcher et al. (2006) and Powell and Letcher (2014).

Order Rhizophydiales Letcher, Mycol. Res. 110:908. 2006

Class Spizellomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554003

Diagnosis: Thallus monocentric, eucarpic; sporangium inoperculate; nucleus of zoospores associated directly or indirectly with kinetosome; rumposomes absent; replacement of the translation elongation factor 1-alpha gene by elongation factor-like gene in genome; mostly saprotrophs in soil and parasites of animals, fungi and stramenopiles. Type: *Spizellomyces* D.J.S. Barr

Remark: The above description is combined from Barr (1980) and Powell and Letcher (2014).

Order Spizellomycetales D.J.S. Barr, Can. J. Bot. 58:2384. 1980

Class Synchronomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554004

Diagnosis: Thallus endobiotic, holocarpic, in a form of a resting spore or sorus surrounded by a membrane, colonial in some stages of development; zoospores posterior, unflagellate; with a single lipid globule surrounded by cisternae of endoplasmic reticulum and microbodies; gamma-like vesicles present; nuclear cap lacking; two kinetosomes almost in parallel, transversely striated; dictyosome solitary, associated with posterior rumposome; flagellar apparatus comprises kinetosome and secondary centriole; flagellar terminal plate biconcave if present; mostly pathogens of terrestrial plants. Type: *Synchytrium* de Bary & Woronin

Remark: The above description is combined from Doweld (2014c) and Powell and Letcher (2014).

Order Synchronomycetes Doweld, Index Fungorum 92:1. 2014
Phylum Monoblepharomycota Doweld, Prosyllabus tracheophytorum: Tentamen systematis plantarum vascularium (Tracheophyta):77. 2001

Subphylum Monoblepharomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554034

Diagnosis: Thallus hyphal, with a foamy appearance due to vacuolated cytoplasm; thalli produce terminal sporangia and are filamentous with a basal holdfast or rhizoidal system; asexual reproduction by zoospores or autospores; zoospores elongate, tapered toward the anterior end, capable of swim; sexual reproduction oogamous by means of posteriorly unflagellate antherozoids borne in antheridia and nonflagellate female gametes borne in oogonia; mostly saprotrophic. Type: *Monoblepharis* Cornu

Remark: The description is adapted from Hibbett et al. (2007) and Karpov et al. (2017a).

Class Monoblepharidomycetes J. H. Schaffn., Ohio Nat. 9:449. 1909

Class Hyaloraphidiomycetes Doweld, Prosyllabus tracheophytorum: Tentamen systematis plantarum vascularium (Tracheophyta):77. 2001

Class Sanchytriomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554005

Diagnosis: Thallus monocentric, epibiotic, penetrates host wall with rhizoid in parasitic species; Sexual reproduction not known; mostly pathogens of freshwater Xanthophyceae algae. Type: *Sanchytrium* Karpov & Aleoshin

Remark: The above description is taken from Karpov et al. (2017a)

Order Sanchytriales Tedersoo et al. *ord. nov.*, Index Fungorum ID: 554006

Diagnosis: As for class. Type: *Sanchytrium* Karpov & Aleoshin

Family Sanchytriaceae Karpov & Aleoshin Fung. Biol. <https://doi.org/10.1016/j.funbio.2017.05.002>.

Phylum Neocallimastigomycota M. J. Powell, Mycol. Res. 111:516. 2007

Subphylum Neocallimastigomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554035

Diagnosis: Thallus monocentric or polycentric, with extensive rhizoids or a bulbous haustorium-like structure; zoospores posteriorly unflagellate or polyflagellate with up to 20 flagella that may adhere together, without nonflagellated centrioles and flagellar props; Asexual reproduction by spherical, oval, or pyriform zoospores that are capable of amoeboid movement; kinetosome present but non-functional centriole absent; mitochondria absent but hydrogenosomes of mitochondrial origin present; anaerobic mostly in digestive system of herbivorous mammals Type: *Neocallimastix* Vavra & Joyon ex I.B. Heath

Remark: This description is adapted from Powell and Letcher (2014).

Class Neocallimastigomycetes M. J. Powell, Mycol. Res. 111:516. 2007

SUBKINGDOM Olpidiomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 554007

Diagnosis: Thallus monocentric, holocarpic or eucarpic, with no hyphae; zoospores posterior, uniflagellate, generally with a single globule, cone-shaped striated rhizoplast fused to both the functional and vestigial kinetosomes, gamma-like particles and rough endoplasmic reticulum; sporangium single, endobiotic; nucleus associated with the basal body, no nuclear cap; two parallel centrioles linked to nucleus by shared, tapering, striated rhizoplast; no root microtubules or dictyosome; side-body complex lacking; pathogens of terrestrial plants. Type: *Olpidium* (A. Braun) J. Schröt.

Remark: Corresponds to Olpidiomycota Doweld. The above description is compiled from Doweld (2013) and Cavalier-Smith (2013).

Phylum Olpidiomycota Doweld, Index Fungorum 42:1. 2013

Subphylum Olpidiomycotina Doweld, Index Fungorum 42: 1. 2013

Class Olpidiomyces Doweld, Index Fungorum 42:1. 2013

SUBKINGDOM Basidiobolomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 554029

Diagnosis: Thallus mycelial, with regular septa or yeast-like cells, uninucleate; nuclei large (often > 10 µm long), with a large central nucleolus; zygosporangia with thick bilayered walls, form homothallically on axis of parental cells; conidiophore simple, with a bulbous swelling below developing conidium; conidia globose, uninucleate, with small basal conical papilla, released by a rocket-like mechanism; saprotrophs or animal pathogens. Type: *Basidiobolus* Eidam

Remark: Corresponds to Basidiobolomycetes sensu Humber (2012). The above description follows Humber (2012)

Phylum Basidiobolomycota Doweld, Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta):77. 2001.

Subphylum Basidiobolomycotina Tedersoo et al. *subphyl. nov.*, Index Fungorum ID: 554036

Diagnosis: As for the subkingdom above. Type: *Basidiobolus* Eidam

Class Basidiobolomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta):77. 2001.

SUBKINGDOM Zoopagomyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 554008

Diagnosis: Thallus mycelial, mostly separated into cells with complete or uniperforate septa; Sexual reproduction, if present, via zygosporangia by gametangial conjugation;

asexual structures may include sporangia, merosporangia, conidia or chlamydospores; saprotrophs, gut symbionts or parasites of animals or mycoparasites. Type: Zoopagomycota Drechsler

Remark: Corresponds to Zoopagomycota M.E. Smith, Spatafora & Stajich. The above description is adopted from Spatafora et al. (2016)

Phylum Entomophthoromycota Humber, Mycotaxon 120:481. 2012, *emend.* Tedersoo et al.

Emendation: Corresponds to Entomophthoromycota Humber but excluding Basidiobolomycetes that is raised to phylum rank because of non-monophyly.

Subphylum Entomophthoromycotina Humber, Mycol. Res. 111: 517. 2007

Class Entomophthoromycetes Humber, Mycotaxon 120:482. 2012

Class Neozygitomycetes Humber, Mycotaxon 120:482. 2012

Remark: Neozygitomycetes are excluded from rRNA gene-based phylogenies because of its extreme divergence. Its position within the Zoopagomycota is not fully resolved (White et al. 2006).

Phylum Kickxellomycota Tedersoo et al. *phyl. nov.*, Index Fungorum ID: 554009

Diagnosis: Thallus arising from a holdfast on other fungi as a haustorial parasite, or branched, septate, subaerial hyphae; mycelium branched or unbranched, regularly septate; septa with median, disciform cavities containing plugs; asexual production by 1- or 2-spored merosporangia, trichospores, or arthrospores; sexual reproduction by zygosporangia that are globose, biconical, or allantoid and coiled; saprotrophs, mycoparasites or obligate symbionts. Type: *Kickxella* Coem.

Remark: The above description is adopted from Hibbett et al. (2007)

Subphylum Kickxellomycotina Benny, Mycol. Res. 111:518. 2007.

Class Kickxellomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554010

Diagnosis: Thallus branched, with septate hyphae giving rise to septate sporangiophores; septa with median disciform cavities containing colorless biconvex or biumbonate plugs that are persistent in 2–3% KOH; asexual reproduction by 1-spored sporangioles formed on pseudophialides that arise from globoid to elongate fertile branchlets termed sporocladia; sexual reproduction by nearly globose zygosporangia; saprobes or weak non-haustorial mycoparasites in soil and dung. Type: *Kickxella* Coem. Remark: The above description is taken from Benjamin (1979).

Order Kickxellales Kreisel ex R. K. Benj., Whole Fungus 2:610. 1979

Class Asellariomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554011

Diagnosis: Thallus branched, filamentous, with harpelloid septa; basal cells for attachment to gut cuticle of a host; no dictyosomes; no zygospores; no sexual reproduction; reproduction via fragmentation of branches into uninucleate arthrospores; habitat in guts of isopods and springtails. Type: *Asellaria* R.A. Poisson

Remark: The above description is taken from Benjamin (1979).

Order Asellariales Manier ex Manier & Lichtw., Mycotaxon 7:442. 1978

Class Barbatosporomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554012

Diagnosis: Thallus branched with a basal cell, bearing trichospores; trichospores cylindrical, without a collar, with multiple fine basal appendages, may bear a cylindrical sleeve or wall at the terminal end, which on dehiscence may reveal appendage-like filaments; zygospores not known; only known from insect gut habitat. Type: *Barbatospora* M.M. White, Siri & Lichtw.

Remark: The above description is taken from Doweld (2014b).

Order Barbatosporales Doweld, Index Fungorum 87:1. 2014

Class Dimargaritomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554013

Diagnosis: Thallus branched, with septate hyphae, producing septate sporangiophores. Septa with median disciform cavities containing colourless, more or less biconvex plugs; plugs with polar protuberances, dissolved in 2% KOH; asexual reproduction by bisporous merosporangia; sexual reproduction by a \pm ornamente zygospore; sporangiola formed on terminal ampullae or on cells of simple or branched fertile branchlets arising from terminal ampullae or in terminal fascicles. Sexual reproduction by subglobose zygospores developed in thin-walled zygosporangia; haustorial mycoparasites of Mucorales and *Chaetomium* spp. Type: *Dimargaris* Tiegh.

Remark: The above description is taken from Benjamin (1979).

Order Dimargaritales R. K. Benj., Whole Fungus 2:607. 1979

Class Harpellomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554014

Diagnosis: Thallus simple or branched, with basal cell attached to the host; hyphae septate; septa contain a lenticular cavity; sexual reproduction via conical or biconical zygospores; asexual reproduction via exogeneous, lateral, elongate monosporous trichospores; endosymbionts of mostly freshwater arthropods. Type: *Harpella* L. Léger & Duboscq.

Remark: The above description is taken from Benjamin (1979).

Order Harpellales Lichtw. & Manier, Mycotaxon 7: 441. 1978

Class Ramicandelaberomycetes Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554015

Diagnosis: Thallus comprised of colourless, septate hyphae; stolons hyaline, septate, forming rhizoids and producing sporangiophores; sporangiophores septate, verticillately branched, forming supporting hyphae that produce rhizoids; branches cylindrical or ellipsoidal, irregularly branching further; sporocladia elongate, attenuate distally, often composed of broadened branches of sporangiophores when ageing; pseudophialides arising from sporocladia and fertile heads, first subspherical, becoming hemispherical, producing sporangioles; sporangioles narrow, fusiform, slightly curved, aseptate, hyaline; sporangial wall adnate to the sporangiospore; zygospores and chlamydospores not known; saprobes in soil. Type: *Ramicandelaber* Y. Ogawa, S. Hayashi, Degawa & Yaguchi

Remark: The above description is taken from Ogawa et al. (2001).

Order Ramicandelaberales Doweld, Index Fungorum 69:1. 2014

Phylum Zoopagomycota M.E. Smith, Spatafora & Stajich, Mycologia 108:1035. 2016, *emend.* Tedersoo et al. Emendation: Corresponds to subphylum Zoopagomycotina Benny that is raised to phylum rank. Other subphyla are transferred to their respective phyla.

Subphylum Zoopagomycotina Benny, Mycol. Res. 111:518. 2007.

Class Zoopagomycetes Doweld, Index Fungorum 60:1. 2014

SUBKINGDOM Mucoromyceta Tedersoo et al. *subkgd. nov.*, Index Fungorum ID: 554016

Diagnosis: Thallus mycelial, with usually broad multinuclear hyphae, septa occurring in separating reproductive cells; sexual reproduction, if present, via zygospores formed by gametangial conjugation; zygospores globose, smooth or ornamented, produced on suspensor cells; asexual reproduction via chlamydospores or sporangiospores produced in sporangia and sporangioles; saprotrophs, plant root symbionts or phytopathogens. Type: *Mucor* Fresen.

Remark: Corresponds to Mucoromycota Doweld as treated in Spatafora et al. (2016).

Phylum Mucoromycota Doweld, Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta):77. 2001, *emend.* Tedersoo et al.

Emendation: Corresponds to Mucoromycotina Benny that is raised to phylum rank. Other subphyla (cf. Spatafora

et al. *Mycologia* 108:1028–1046. 2016) are assigned to separate phyla.

Subphylum Mucoromycotina Benny, *Mycol. Res.* 111:517. 2006

Class Mucoromycetes Doweld, *Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta)*:77. 2001

Remark: Corresponds to Mucorales Fr., *Syst. Mycol.* 3:296. 1832. *Emend.* Spatafora et al. *Mycologia* 108:1035. 2016

Class Endogonomycetes Doweld, *Index Fungorum* 57:1. 2014

Class Umbelopsidomycetes Tedersoo et al. *cl. nov.*, *Index Fungorum* ID: 554017

Diagnosis: Thallus branched; hyphae initially without septa but developing near the branching; relatively slow growth in culture media; Asexual reproduction via sporangia; sporangiophores densely branched, with septa distant from the sporangium; sporangia reddish or ochraceous, globose or elongate, multispored or single-spored; columella usually conspicuous; spores of various shape and pigmentation; chlamydospores abundant, filled with lipids in culture; no zygospores; no sexual reproduction. Type: *Umbelopsis* Amos & H.L. Barnett

Remark: The above description is taken from Spatafora et al. (2016).

Order Umbelopsidales Spatafora & Stajich, *Mycologia* 108:1035. 2016

Phylum Mortierellomycota Tedersoo et al. *phyl. nov.*, *Index Fungorum* ID: 554018

Diagnosis: Thallus with dichotomously branching, anastomosing hyphae, bearing stylospores; Sporangiophores initially coenocytic, irregularly septated when mature; asexual reproduction via sporangia and sporangioles; sporangia spherical, multi-spored; no columella; sporangioles terminal, borne on erecting hyphae; Spores ellipsoid or globose or irregular, smooth or ornamented; zygospores naked; mostly saprotrophs in soil. Type: *Mortierella* Coem.

Remark: Corresponds to Mortierellomycotina Kerst. Hoffm., K. Voigt & P.M. Kirk. The above description is taken from Hoffmann et al. (2011) and Doweld (2014a).

Subphylum Mortierellomycotina Kerst. Hoffm., K. Voigt & P.M. Kirk, *Mycotaxon* 115:360. 2011

Class Mortierellomycetes Doweld, *Index Fungorum* 46:1. 2014

Phylum Calcarisporiellomycota Tedersoo et al. *phyl. nov.*, *Index Fungorum* ID: 554019

Diagnosis: Thallus branched, with septate hyphae; vegetative hyphae hyaline, smooth, thin-walled; cultures with no distinctive smell; sporangiophores (if present) simple, hyaline, smooth, arising from undifferentiated hyphae; sporangia unispored, ellipsoid, with or without a small columella; spores uninucleate, hyaline, smooth, thin-

walled, ovoid to ellipsoid, with a rounded base; chlamydospores (if present) born laterally on short hyphae, 1-celled, elongate to globose, thick-walled, spiny; sexual cycle not known; saprotrophic in soil, non-nematophagous. Type: *Calcarisporiella* de Hoog

Remark: The above description is combined from Hirose et al. (2012) and Jiang et al. (2011).

Subphylum Calcarisporiellomycotina Tedersoo et al. *subphyl. nov.*, *Index Fungorum* ID: 554037

Diagnosis: As for the phylum above. Type: *Calcarisporiella* de Hoog

Class Calcarisporiellomycetes Tedersoo et al. *cl. nov.*, *Index Fungorum* ID: 554020

Diagnosis: As for phylum above. Type: *Calcarisporiella* de Hoog

Order Calcarisporiellales Tedersoo et al. *ord. nov.*, *Index Fungorum* ID: 554021

Diagnosis: As for phylum above. Type: *Calcarisporiella* de Hoog

Family Calcarisporiellaceae Tedersoo et al. *fam. nov.*, *Index Fungorum* ID: 554022

Diagnosis: As for phylum above. Type: *Calcarisporiella* de Hoog

Genus *Calcarisporiella* de Hoog, *Studies in Mycology* 7:68. 1974

Genus *Echinochlamydosporium* X.Z. Jiang, H.Y. Yu, M.C. Xiang, X.Y. Liu & X.Z. Liu, *Fung. Div.* 46:46. 2011

Phylum Glomeromycota C. Walker & A. Schüßler, *Mycol. Res.* 105:1416. 2001

Subphylum Glomeromycotina Spatafora & Stajich, *Mycologia* 108: 1034. 2016

Class Glomeromycetes Caval.-Sm., *Biol. Rev.* 73:246. 1998 (as “Glomomycetes”), *emend.* Oehl, G.A. Silva, B.T. Goto & Sieverd., *Mycotaxon* 116:372. 2011

Class Archaeosporomycetes Sieverd., G.A. Silva, B.T. Goto & Oehl, *Mycotaxon* 116:374. 2011

Class Paraglomeromycetes Oehl, G.A. Silva, B.T. Goto & Sieverd., *Mycotaxon* 116:374. 2011

SUBKINGDOM Dikarya Hibbett, T.Y. James & Vilgalys, *Mycol. Res.* 111:518. 2007, *emend.* Tedersoo et al. Emendation: The Dikarya includes the phylum Entorrhizomycota R. Bauer, Garnica, Oberw., K. Riess, M. Weiß & Begerow because of dikaryotic hyphae and sister position to Ascomycota and Basidiomycota combined.

Remark: We endorse using Dikarya rather than Dikaryomycota, Dikaryomycota or Neomycota for consistency.

Phylum Entorrhizomycota R. Bauer, Garnica, Oberw., K. Riess, M. Weiß & Begerow, *PLoS One* 10:e0128183:10. 2015

Subphylum Entorrhizomycotina Tedersoo et al. *subphyl. nov.*, *Index Fungorum* ID: 554039

Diagnosis: Thallus hyphal inside host tissue, forming intracellular septate coils bearing terminal teliospores that

germinate internally by becoming four-celled; hyphae with regular septa, with or rarely without dolipores, without Woronin bodies or membrane caps; haustoria present; phytoparasitic by forming root galls in Cyperaceae or Juncaceae or rarely in eudicyledons. Type: *Entorrhiza* C.A. Weber

Class Entorrhizomycetes Begerow, Stoll & R. Bauer, *Mycologia* 98:908. 2006

Phylum Basidiomycota R.H. Whittaker ex Moore, *Bot. Mar.* 23:371. 1980

Subphylum Agaricomycotina Doweld, *Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta)*:77. 2001

Class Agaricomycetes Doweld, *Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta)*:77. 2001

Class Dacrymycetes Doweld, *Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta)*:77. 2001

Class Tremellomycetes Doweld, *Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta)*:77. 2001

Subphylum Pucciniomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5: 45. 2006

Class Agaricostilbomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:45. 2006

Class Atractiellomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:45. 2006

Class Classiculomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:46. 2006

Class Cryptomycocolacomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:46. 2006

Class Cystobasidiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:46. 2006

Class Microbotryomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:47. 2006

Class Mixiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:47. 2006

Class Pucciniomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:48. 2006

Class Spiculogloeomycetes Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Stud. Mycol.* 81:172. 2015

Class Tiritrachiomycetes Aime & Schell, *Mycologia* 103:1339. 2011

Subphylum Ustilaginomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., *Mycol. Progr.* 5:45. 2006

Class Exobasidiomycetes Begerow, M. Stoll, R. Bauer, *Mycologia* 98:908. 2006

Class Malasseziomycetes Boekhout, Q.M. Wang & F.Y. Bai, *Persoonia* 33:46. 2014

Class Moniliellomycetes Q.M. Wang, F.Y. Bai & Boekhout, *Persoonia* 33:46. 2014

Class Ustilaginomycetes R. Bauer, Oberw. & Vánky, *Can J Bot* 75:1311. 1997

Subphylum Wallemiomycotina Doweld, *Index Fungorum* 73:1. 2014

Class Geminibasidiomycetes H.D.T. Nguyen & Seifert, *IMA Fungus* 6:228. 2015

Class Wallemiomycetes Zalar, de Hoog & Schroers, *Ant. van Leeuw.* 87:322. 2005

Phylum Ascomycota R.H. Whittaker, *Quart. Rev. Biol.* 34:220. 1959

Subphylum Pezizomycotina O.E. Erikss. & Winka, *Myconet* 1:9. 1997

Class Arthoniomycetes O.E. Erikss. & Winka, *Myconet* 1:4. 1997

Class Collemopsidiomycetes Tedersoo et al. *cl. nov.*, *Index Fungorum* ID: 554023

Diagnosis: Thallus comprised of fine hyphae loosely associated with Cyanobacteria and developing ascomata; ascomata perithecioid, solitary, unilocular, with a carbonized to hyaline exciple; branched and anastomosing, often irregularly thick, net-like physes; asci bitunicate, fissitunicate, with ocular chamber, ovoid to subcylindrical, usually stalked; ascospores hyaline (rarely brownish in mature specimens), oblong to ovoid-fusiform, 1-septate, with gelatinous perispore usually present; conidiomata pycnidial; conidiogenous cells cylindrical; conidiogenesis phialidic; conidia bacilliform to ellipsoid; lichenized and lichenicolous fungi with crustose, epilithic or endolithic, or lichenicolous forms and Cyanobacteria as photobionts Type: *Collemopsidium* Nyl.

Order Collemopsidiales Pérez-Ortega, Garrido-Benavent & Grube, *Fung. Div.* 80:296. 2016

Class Coniocybomycetes M. Prieto & Wedin, *Cladistics* 29:305. 2013

Class Dothideomycetes O.E. Erikss. & Winka, *Myconet* 1:5. 1997

Class Eurotiomycetes O.E. Erikss. & Winka, *Myconet* 1:6. 1997

Class Geoglossomycetes Zheng Wang, C.L. Schoch & Spatafora, *Persoonia* 22:131. 2009

Class Laboulbeniomycetes Engl., *Natürl. Pflanzenfam.* 6. 1897

Class Lecanoromycetes O.E. Erikss. & Winka, *Myconet* 1:7. 1997

Class Leotiomycetes O.E. Erikss. & Winka, *Myconet* 1:7. 1997

Class Lichinomycetes Reeb, Lutzoni & Cl. Roux, *Mol Phyl Evol* 32:1055. 2004

Class Orbiliomycetes O.E. Erikss. & Baral, *Myconet* 9:96. 2003

Class Pezizomycetes O.E. Erikss. & Winka, *Myconet* 1:8. 1997

Class Sordariomycetes O.E. Erikss. & Winka, Myconet 1:10. 1997

Class Xylonomycetes R. Gazis & P. Chaverri, Mol Phyl Evol 65:301. 2012

Subphylum Taphrinomycotina O.E. Erikss. & Winka, Myconet 1:11. 1997

Class Archaeorhizomycetes Rosling & T. James, Science New York 333:879. 2011

Class Neoelectromycetes O.E. Erikss. & Winka, Myconet 1:8. 1997

Class Pneumocystidomycetes O.E. Erikss. & Winka, Myconet 1:9. 1997

Class Schizosaccharomycetes O.E. Erikss. & Winka, Myconet 1:10. 1997

Class Taphrinomycetes O.E. Erikss. & Winka, Myconet 1:11. 1997

Subphylum Saccharomycotina O.E. Erikss. & Winka, Myconet 1:9. 1997

Class Saccharomycetes O.E. Erikss. & Winka, Myconet 1:10. 1997

KINGDOM Nucleariæ Tedersoo et al. *kgd. nov.*, Index Fungorum ID: 554024

Diagnosis: Vegetative cells amoeboid, with rounded body and filopodes; flat discoid mitochondrial cristae; feeding by ingestion of various microorganisms. Type: *Nuclearia* Cienkowski

Phylum Nuclearida Tedersoo et al. *phyl. nov.*, Index Fungorum ID: 554025

Diagnosis: Vegetative cells amoeboid, naked, solitary, with rounded body and elongated filopodes; not forming fruiting bodies; uninucleate or multinucleate; moving by attachment and subsequent shortening of filopodes; flat discoid mitochondrial cristae; feeding by ingestions of small organisms, including algal filaments; reproductive cysts not known. Type: *Nuclearia* Cienkowski

Class Nucleariæ Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554026

Diagnosis: As for phylum above. Type: *Nuclearia* Cienkowski

Order Nucleariida Caval-Sm., Microbiol. Rev. 57:988. 1993

Phylum Fonticulida Tedersoo et al. *phyl. nov.*, Index Fungorum ID: 554027

Diagnosis: Vegetative cells amoeboid with rounded spherical body and extending filopodes; cells sorocarpic, aggregating to form a hollow gelatinous extracellular stalk supported by fibrillar matrix material; stalked fruiting bodies bear a sorus with multiple spores that are forcibly erupted; Myxamoebae may encyst in situ as rounded microcysts; flat discoid mitochondrial cristae; feeding by ingestion of bacterial cells; known from soil and dung. Type: *Fonticula* Worley, Raper & Hohl.

Class Fonticulæ Tedersoo et al. *cl. nov.*, Index Fungorum ID: 554028

Diagnosis: As for phylum above. Type: *Fonticula* Worley, Raper & Hohl.

Order Fonticulida Caval-Sm., Microbiol. Rev. 57:988. 1993

Remark: The names of Nucleariæ and its constituent taxa are not being treated here as Fungi for nomenclatural purposes, but the names are nevertheless registered with Index Fungorum.

SUPERKINGDOM Holozoa B.F. Lang et al. Curr. Biol. 12:1776. 2002

Evolutionary ecological analyses

Based on the updated fungal classification framework of nine subkingdoms, 18 phyla, 23 subphyla, 74 classes, 215 orders, 731 families and 5377 genera, we generated an analytical tool, which enables to perform simple evolutionary ecological analyses. The perl script taxonomy_to_tree.pl maps Species Hypotheses to the existing taxonomic framework within seconds by omitting resource-consuming alignment and phylogenetic analyses with nucleotide and amino acid sequences. In principle, the tool can be used to link any OTU taxonomy matrix (cf. Fig. 2) to custom classification system to prepare a newick-formatted tree for statistical testing. These analyses enable to test hypotheses about differences in (1) phylogenetic diversity, (2) phylogenetic community turnover and (3) phylogenetic community organisation (phylogenetic overdispersal vs. conservation). The two main drawbacks of this method are (1) the lack of resolution at nodes that are divided into > 2 subtaxa, and (2) the lack of branch length information. For example, the method does not distinguish between the order of divergence of Pezizomycotina classes, or it does not account for the long branches of Zoopagomyceta and Microsporidea. However, given the calibration to divergence time, the standardisation of branch length can be beneficial on many occasions. Nonetheless, because of these approximations, analyses of trait evolution, diversification and ancestral states cannot be performed with the Fungi_TH_1.1 data set.

Evolutionary ecological analyses are more powerful when using either (1) real community sequence data (e.g. Schadt et al. 2003; Veldre et al. 2013) or (2) community taxonomic data mapped onto sequence-based phylogenies (Branco 2010; Fouquier et al. 2016). Use of original sequence data would require utilisation of a genetic marker that is alignable across the entire target group and thus the ITS barcode would be usually restricted to genus or family-level analyses. The more readily alignable 18S and 28S rRNA genes tend to lack resolution at the level of species

and functional groups by lumping ectomycorrhizal and saprotrophic fungal species in many cases. The alternative options include use of protein-encoding gene barcodes such as RPB2 (Vetrovsky et al. 2016) or a long barcode spanning ITS and 18S or 28S (Timling et al. 2014; Tedersoo et al. 2017, 2018). Mapping of OTUs to sequence-based phylogenies is difficult, because it essentially assumes building a backbone phylogeny that spans all genera of fungi and construction of multiple small trees associated to the backbone. The backbone would be limited to taxa that have a representative gene sequence present in databases and assignable to a coherent set of ITS sequences (Fouquier et al. 2016). In large-scale studies, nearly half of all taxa cannot be assigned to described genera (Tedersoo et al. 2014). Because the relationships of these unassigned taxa to 18S/28S rRNA gene backbone cannot be determined, these taxa need to be excluded from construction of hybrid phylogenies. In addition, comparable sequence data for 18S and 28S rRNA genes does not exist for most ascomycete and basidiomycete genera.

Testing the `taxonomy_to_tree.pl` script on a global soil fungal OTU taxonomy matrix enabled to construct a rough phylogenetic tree in 1 s using an ordinary laptop computer. The analyses revealed that while OTU richness is greatest in tropical forest biomes and lowest in grassy biomes (Tedersoo et al. 2014), PD_{OTU} and UNI_{OTU} are greatest in the grasslands and shrublands biome but lowest in temperate and boreal forest biomes (Fig. 7a–c). The NRI indicated that fungal communities in all biomes are phylogenetically clustered (Fig. 7d). By contrast, the NTI revealed that tropical forest and savanna biomes were significantly phylogenetically clustered and only southern temperate forests are phylogenetically overdispersed (Fig. 7e). These differences in NTI and NRI suggest that southern temperate forest sites harbour relatively fewer congeneric (and confamilial) relatives, whereas tropical lowland forests stand out by more even distribution of higher-ranking taxa. The low taxonomic but high phylogenetic diversity of grassy habitats reflects both high proportion of OTUs belonging to early diverging fungal lineages and low paucity of OTUs belonging to hyperdiverse EcM fungal genera. Taken together, the main benefits of the proposed approach include taxonomic coverage of all OTUs assignable to fungi, simple and rapid tree construction as well as understanding phylogenetic perspectives on community composition.

Conclusions

We propose an alternative higher-level classification of Fungi based on the criteria of monophyly and comparable divergence times to provide a more natural classification

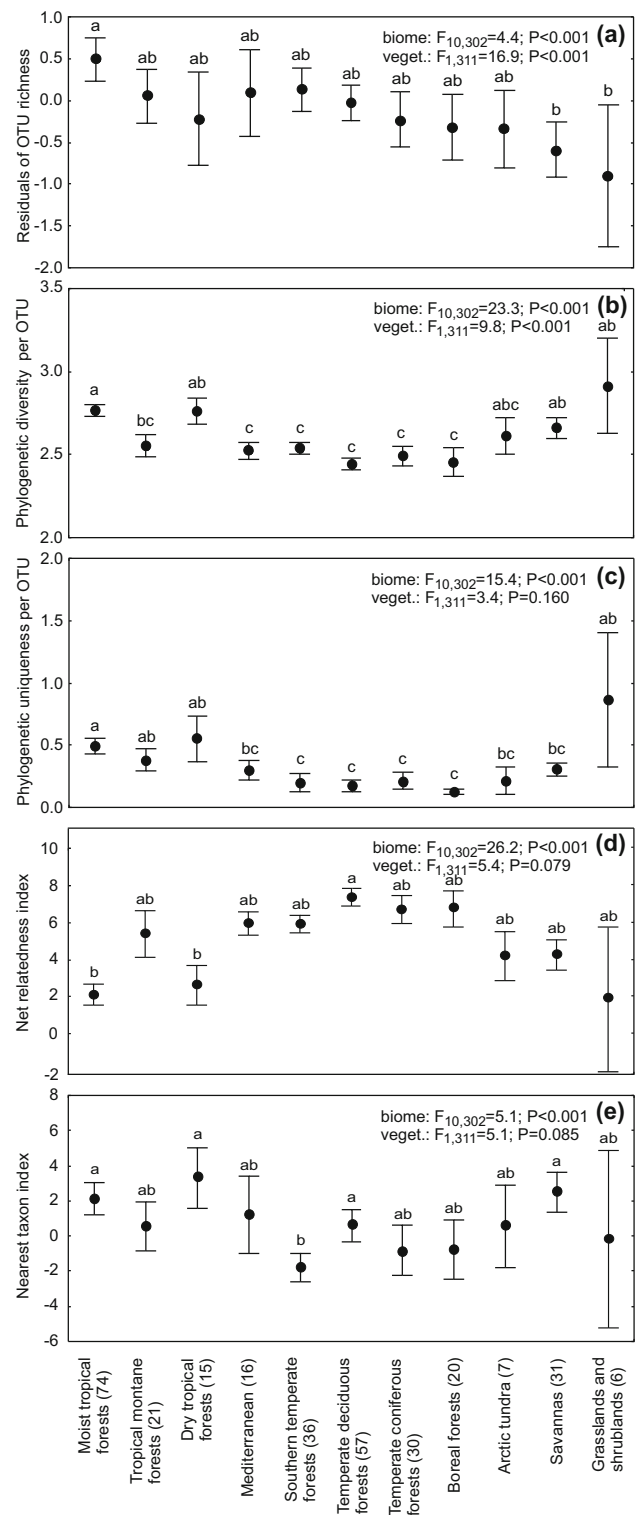


Fig. 7 Example of use of the `taxonomy_to_tree.pl` script for fungal hierarchical phylogeny: differences in **a** fungal OTU richness (standardized residuals), **b** phylogenetic diversity per fungal OTU (PD_{OTU}), **c** uniqueness (UNI_{OTU}), **d** net relatedness index (NRI) and **e** nearest taxon index (NTI) of the world's biomes. Taxonomic data and OTU distribution data are updated from Tedersoo et al. (2014)

and improve the taxonomic and phylogenetic precision in evolutionary ecological and biodiversity analyses. To enable such analyses, we provide a taxonomy_to_tree.pl script and a backbone classification tree. The script can be used for communities of any organisms with elaborate hierarchical classification schemes.

Because our fungal classification is built on rRNA genes with some support from two protein-encoding genes, we anticipate that the order and time of divergence of the main fungal groups remain to be resolved using phylogenomics approach with much improved taxon sampling (Torruella et al. 2017; McCarthy and Fitzpatrick 2017). We advocate that single-cell genomics analyses offer great promise for generating genome data from members of the unnamed phyla and potentially unculturable early diverging fungal lineages (Seeleuthner et al. 2018).

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Author contributions L.T. directed the project and wrote the manuscript with input from other authors. U.K. developed the T.H. concept with K.A., M.D. and D.S. putting it into practice. L.T., T.M. and U.K. proposed an update to the classification and discussed the ideas with scientific community. M.R. generated the perl script. M.B. performed evolutionary ecological analyses. S.S.-R. constructed dated phylogenies.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interests and confirm full compliance to research ethics.

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